A SINUS-BEARING MONOPLACOPHORAN
AND ITS ROLE IN THE CLASSIFICATION
OF PRIMITIVE MOLLUSCS

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ABSTRACT. The discovery of symmetrically disposed multiple muscle scars in *Bellerophon acutilira* Hall, a middle Devonian form assigned to the bellerophontoid genus *Sinuitopsis* Perner, indicates that *Sinuitopsis* is a cyclomyan monoplacophoran. Deployment of the muscle scars shows affinity with the cyclomyan genera *Yochelsonellis* (Horný) and *Cyrtolites* Conrad. A ridge-furrow complex is interpreted as a reflection on the inside of the shell of a dorsally situated rectal tract. The presence of a deep anal sinus and notch in *S. acutilira* demands a reconsideration of monoplacophoran-gastropod relationships. Such a sinus or slit can no longer be always considered anterior, and thus, evidence of torsion in fossil archeogastropods. Quite possibly sinus-bearing cyclomyans were the direct ancestors of the primitive archeogastropods (i.e. the Bellerophontina). The use of the sinus as a tool for the recognition of bellerophontids is discouraged in favour of parietal deposits and posterior trains. A posterior anal sinus was probably advantageous in the achievement of maximum separation of respiratory currents and excretory products.

No molluscan group has provided more controversy and speculation than the bellerophontoids (here including the 'true' bellerophontids and the coiled monoplacophorans), with the exception of such enigmatic Cambrian miscellanea as *Matthevia*. Historically, the main problem has been whether or not these bilaterally symmetrical and isostrophically coiled forms were gastropods, i.e. had undergone the process of torsion. Two schools of thought have developed. Wenz (1938), Moore (1952), and others were convinced that the bellerophontoids were untorted forms. Their ideas were based, in part, on recapitulatory concepts of Naef (1913) and others who stated that, since the ontogenetic development of the gastropods clearly show that larval torsion is linked to the assumption of an asymmetrical shell, the same process must have occurred in the phylogeny of the gastropods. Thus, since the bellerophontoids are symmetrical, they did not undergo torsion. This concept was formalized by Simroth (1906), who erected the class Amphigastropoda for the bellerophontoids, and later modified by Thiele (1935). Crofts (1955) has shown in her brilliant studies of *Haliotis* that torsion and asymmetry in fact are separate ontogenetic processes and that torsion itself is a gradational process. In consequence we feel that the original concept of this school is considerably weakened.

The other school, maintained by J. B. Knight (1952), Yonge (1947, 1960), and others, was of the opinion that the bellerophontids had, in fact, undergone torsion. Three lines of evidence were cited. Their most compelling argument was that the bellerophontids possess an anal sinus or slit in the plane of symmetry and such an attribute would have been unnecessary in an untorted form since the mantle cavity with the anus, ctenidia, and associated organs was posterior, posing no threat of fouling. Secondly, bellerophontids possess parietal deposits which could not form if the head were lying beneath the earlier whorls. Finally, the primitive forms have an elongate trail which would impede the manoeuvrability of the protracted head. An additional piece of evidence was described by Knight (1941b) when he illustrated, in a restoration of the genus *Knightites*, functional

inhalant siphons on either side of the anal slit, making mandatory the assumption that the mantle cavity lay in an anterior (torted) position.

No fruitful purpose would be served here by undertaking a detailed review of the history of various theories regarding the development of torsion and coiling (but see Knight *et al.* 1960, Ghiselin 1966, Batten, Rollins, and Gould 1967). It is germain to say, however, that we should not eliminate speculation until a living bellerophont is found. Some light can be shed on the problem by examining some new facts that have recently come to light as a by-product of the intense study of the monoplacophorans and bellero-phontids, notably by R. Horný of Praha (Horný, 1963–5).

Horný has presented a modified classification of the monoplacophorans based primarily on the shape, distribution, and number of paired muscle scars in relation to the apex. He has suggested that evolution and taxonomic diversity are greater in this group than originally believed. It is interesting to note that those taxa possessing the greatest number of muscle scar pairs are patelliform and morphologically the most primitive, and that the cyclomyans, which are coiled and may have fused lateral muscles, are probably the most advanced and had greater survival value.

In a paper dealing with the bellerophontid classification Horný (1963) described a number of variations in the shapes of sinuses and slits. He alluded to the possibility that these patterns may be useful in classification. In scanning the morphological range through the course of bellerophontid diversification, with Horný's allusion in mind, we have been struck by several rather consistent distributions. Primitive bellerophontids, with some exceptions, have rather shallow sinuses and slits. This has been noted before and at least one evolutionary trend is based on the deepening of the slit through time. However, along with the shallowness of the sinus and slit we have observed that the majority of these primitive forms lack parietal deposits, and in only a few forms, such as *Anconochilus*, is a trail developed which would impede the organism during the pro-tractile stage.

Our contention, evidence for which is cited below, is this: those bellerophontids which possess sinuses or slits, lateral columellar retractor muscles, parietal deposits, posterior trails, platforms, and/or other similar apertural modifications (see Rollins 1966) are true gastropods. Horný (1965a) has constructed the monoplacophoran subclass Cyclo-mya to include coiled bilaterally symmetrical forms which possess multiple pairs of muscle scars (which may be fused). We would emend his definition to include those forms which, in addition, have a sinus or slit. Primitive bellerophontids similar to *Sinuitopsis*, which have a sinus and no parietal inductura, might well prove to be Monoplacophora. It is possible that a search through the bellerophontid families will reveal more of these sinuate cyclomyans.

On the basis of the discovery of symmetrical, multiple and partially fused muscle scars in sinus-bearing *Sinuitopsis acutilira* (Hall) from middle Devonian rocks, a new inter-pretation for the origin of the Gastropoda is now possible.

Previously, it had been stated that torsion occurred and then a sinus-slit developed, presumably for sanitary efficiency. Our hypothesis is that the sinus-slit developed *prior* to torsion and only because it did exist when torsion occurred was viability and a positive selective advantage assured.

With the picture just developed, a reasonable conclusion to come to is that the sinuate cyclomyans originated during the Cambrian, gave rise to the true gastropods

and that phylogenetic diversification developed in both groups. However, in reviewing the genera of primitive Gastropoda in the Cambrian through Devonian, we have been forcibly struck by the fact that the Cambrian bellerophontids, for example, are distinct and do not seem to be ancestral or related to later genera. It appears that the Ordovician and Silurian genera are equally unrelated to the Devonian forms.

The phylogenetic picture, as we envisage it, is the development of a sinus in middle Cambrian cyclomyans which in turn were ancestral to the first bellerophontid and pleuro-tomarian gastropods. Following this Cambrian event, another sinuate cyclomyan group appeared giving rise to the Ordovician and Silurian primitive gastropods. The final iterative phase occurred in the Devonian when yet another sinuate cyclomyan group, or a surviving group, originated gastropod groups which underwent a very rapid period of adaptive radiation. This picture appears more consistent with the fossil record and helps explain the large morphological gaps between families of bellerophontids, but, of course, it does admit a polyphyletic origin of the gastropods. We are advancing this different hypothesis for the origin of some of the primitive gastropods in order to stimulate discussion and further testing. We do not wish, at this time, to discuss the various ideas regarding the origin of the pleurotomarians. We suspect that, rather than being derived from the bellerophontids as Knight (1952) has suggested, they were derived directly from the cyclomyans. Consideration of some of these statements will appear in subsequent papers by the authors.

From the evidence of the reduction of symmetrical multiple paired muscles scars and the development of cyclomyan reduced or fused musculature, we are convinced that there was a concomitant reduction in the associated multiple paired organs. This, coupled with the trend in the cyclomyans for increased coiling, accounts for the confusing convergence upon the bellerophontids.

SYSTEMATIC DESCRIPTION

Class MONOPLACOPHORA Wenz in Knight 1952
Subclass CYCLOMYA Horný 1965
Order CYRTONELLIDA Horný 1963
Superfamily CYRTOLITACEA S. A. Miller 1889
Family CYRTOLITIDAE S. A. Miller 1889
? Subfamily CYRTOLITINAE S. A. Miller 1889
Genus SINUITOPSIS Perner 1903

Sinuitopsis acutilira (Hall)

Plate 28, figs. 1–8

Fig. 1–8, *Sinuitopsis acutilira* (Hall). 1–2, USNM 156725, dorsal and oblique lateral views showing discrete dorsal pair of muscle scars and partially fused right lateral and right ventral muscle scars ×3. 3. paralectotype AMNH 28470, dorsal view of one of Hall's types showing nature of sinus and notch ×4. 4. AMNH 28469, dorsal view showing muscle scars, 'migration tracks', and ridge-furrow complex ×3. 5. USNM 156723, latex mould of dorsal muscle scar pair and ridge-furrow complex ×3·5. 6, 8. USNM 156722, posterior dorsal and lateral views showing sinus and umbilicus 6, ×2, 8, ×3. 7. USNM 156724, dorsal view showing muscle scar and sinus ×4.
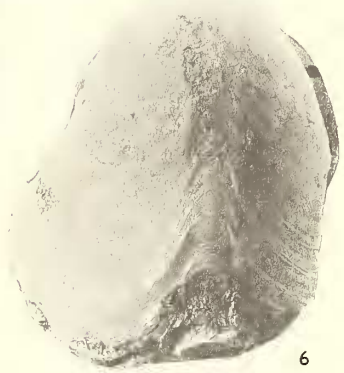
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1861 *Bellerophon acutilira* Hall, p. 28 (also 1876, Pl. 25, figs. 19–21 and 1879, p. 106, pl. 25, figs. 4–8).

Description. Large symmetrically coiled monoplacophorans with a deep obtusely V-shaped posterior sinus, three pairs of prominent muscle scars arranged in a posterior field, and a possible obscure second anterior field of scars; in main field dorsal pair most distinct, depressed, slightly ovoid in outline, and symmetrically placed anteriorly on either side of medial ridge-furrow complex; lateral scars situated anterior to dorsal scars, elongate in outline, depressed, and often composed of at least two centrally fused parts; lateroventral scars obscure, depressed, slightly anterior to lateral pair, elongate, and may consist of two or more fused parts; possibly secondary anterior field extremely obscure, with variable number of pits or depressions on steinkern, and no distinct positional patterns; growth structures on muscle scars suggested but not clearly defined; 'migration tracks' usually well developed and complex, typically extending posteriorly from margins of main field muscle scars; the medial dorsal ridge-furrow complex extends on steinkerns from a point just posterior to the main field dorsal scars to the apex of the posterior sinus, which is usually reflected on the steinkern as a V-shaped elevated area; rapidly expanding whorls slightly impressed, profile bluntly rounded dorsally, gently convex laterally, but entering the deep open umbilicus with a moderately sharp ventral flexure; aperture rather wide, lateral lips rounded, but not lobe-like; posterior sinus deep and roundly V-shaped terminating in a rounded notch; ornament dominantly collabral, with closely spaced growth-lines often fused into thicker growth increments; faint spiral ornament sometimes visible, primarily on the lateral whorl slopes; parietal and columellar inducturas absent; shell microstructure imperfectly known, apparently a combination of prismatic and lamellar.

Discussion. The type specimens of *S. acutilira* (Hall) bear the locality label, Hamilton Group, Madison County, New York, and are poorly preserved composite moulds, most of them moderately compressed. Nevertheless, there is little doubt that they are conspecific with the individuals from the Pompey member of the Skaneateles formation near Morrisville, New York. The two samples are identical in details of shell morphology, but Hall's specimens are uniformly of smaller size.

In the literature *Sinuitopsis* has formerly been reported only from the Ordovician of Bohemia and north-east Asia. Horný (1963) has most recently dealt with the species of *Sinuitopsis* and has concluded primarily from the lack of lateral apertural lobes that *Sinuitopsis* is indeed quite far removed from the genus *Sinuites*, to which it bears a superficial resemblance. At that time, *Sinuitopsis* was generally considered a subgenus of *Sinuites* (Knight *et al.* 1960).

Although Horný did not find muscle scars on the Bohemian representatives of *Sinuitopsis*, the material is reported to be rather poorly preserved and it is probable that future investigations will show the Bohemian species to be monoplacophorans. Perner (1903) reported and figured dorsal nodes in *Sinuitopsis nodosa* Perner which, according to Horný, occur sporadically and only in some specimens. Perhaps these nodes are muscle scars. It is significant that the Bohemian species also lack parietal inductura deposits.

S. acutilira (Hall) is very similar in external morphology to the Bohemian species,

S. neglecta Perner, *S. nodosa* Perner, and *S. hornýi* Marek, usually differing only in small details of ornament and degree of circumumbilical angulation.

Measurements.

	Total width (mm.)	Total height (mm.)
USNM 156723	17·70	25·00
USNM 156724	17·25*	21·15*
USNM 156725	16·70	20·95*
AMNH 28469	17·40	20·90*
,,	18·75	22·90*
,,	18·80	23·70
,,	20·00*	24·90
,,	16·75*	21·70
,,	20·55	23·45
,,	—	20·10
,,	20·45*	27·55*

* Estimated.

Material. Sixteen specimens from the Pompey member of the Skaneateles formation in central New York State, U.S.A. Fifteen specimens were obtained from exposures along Electric Light Stream, two miles south-west of Morrisville, Madison County, N.Y. One specimen is from Pratts Falls, five miles south of Manlius, Onondaga County, N.Y.

Depositories. American Museum of Natural History, New York, N.Y. (AMNH) and U.S. National Museum, Washington, D.C. (USNM).

ANATOMY AND FUNCTIONAL MORPHOLOGY OF
SINUITOPSIS ACUTILIRA (HALL)

Muscle-field(s). Symmetrical multiple muscle pairs, of the pattern displayed by *S. acutilira*, have been observed on other planispirally coiled fossil molluscs and have been used as evidence for non-torsion. The occurrence of multiple muscle pairs, coupled with the lack of an anal sinus, has led to the assignment of these closely related lower Palaeozoic molluscs to a specialized subclass of monoplacophorans, the Cyclomya (Horný 1965a). Among the better-known cyclomyans, *Yochelsonellis*, *Cyrtolites*, and *Sinuitopsis*, there is a high degree of similarity in muscle emphasis and position.

In the three cyclomyan genera mentioned above, the dorsal muscle scar pair of the main field is deep and very distinct, suggesting strong retractor muscle emplacements. The other pairs of the main field are always less distinct, often fused, and located laterally or even ventrally on the shell. Functionally, they seem best explained as subsidiary pedal retractors. However, the arrangement of the muscle scars in *S. acutilira* might preclude the possibility that they functioned as pedal retractors. Pedal retractors in gastropods are anchored in the columellar region to provide maximum leverage for rapid retraction or protraction of the foot mass. An alternative functional explanation of these muscle pairs involves their use not as retractors but merely as pedal muscles positioning and drawing the shell down over the head-foot mass. However, the sinuous shape (at least in *Sinuitopsis*), and unexpanded nature of the aperture, coupled with the large planispiral shell and centralized mantle cavity, would make a limpet-like habitat very unlikely in these forms. A third possibility would be the use of the muscle-field solely in

pedal positioning, implying a large protruded foot mass and, possibly, a highly specialized locomotory behaviour. Unfortunately, we are unable at this time to speculate constructively upon the special function of the second less distinct muscle field of the cyclomyans. It is important to note, however, that *S. acutilira* reaffirms a major phylogenetic trend of the cyclomyans, the general reduction and fusion of muscle pairs (Horný 1965*b*).
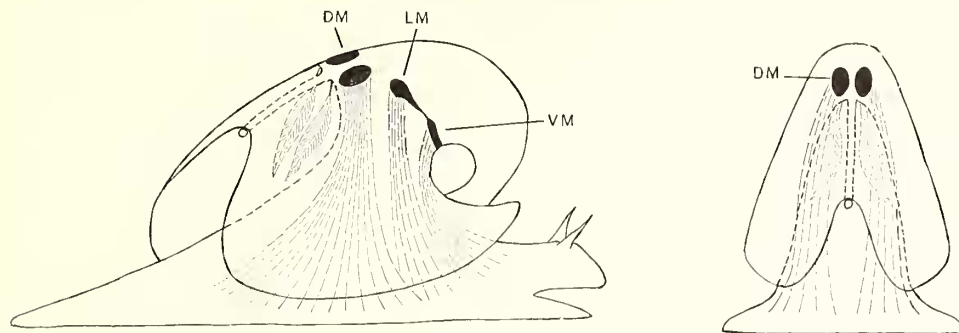
TEXT-FIG. 1. Hypothetical reconstruction of *Sinuitopsis acutilira* (Hall); lateral (left diagram) and posterior (right diagram) views. Muscle scars in solid black. DM = dorsal retractor muscle scar pair, LM = right lateral retractor muscle scar, VM = right latero-ventral retractor muscle scar.

The relation of multiple muscle pairs to the question of torsion in these forms will be considered in a later section.

Ridge-furrow complex. The dorsal ridge-furrow complex of *Sinuitopsis* is not unique to that genus, for a strikingly similar feature occurs in a Bohemian cyclomyan, *Yochelsonellis*. In both genera the complex extends adapically (anteriorly) along a medio-dorsal line, terminating between or immediately posterior to the prominent dorsal muscle scars. The sudden disappearance of the ridge-furrow complex anteriorly probably denotes the extremity of the mantle cavity. Visualization of this feature on the inside of the shell of *Sinuitopsis* suggests a medial trough formed by lateral secondary shell deposition, probably resulting from reflection of the mantle over a dorsally situated rectal-hypobranchial gland system.

Steinkerns of *Cyrtolites ornatus* Conrad display an accentuated medio-dorsal angulation on the adult whorl also immediately posterior to the main dorsal muscle scars. Conceivably, this angulation reflects a trough on the inner shell surface with a function analogous to that of *Sinuitopsis* and *Yochelsonellis*. Similar furrows or troughs in the presumed position of the anus are known in some gastropod groups (e.g. the euomphalids). Maximum separation within the mantle cavity of the anus and the ctenidia may have been functionally advantageous to the cyclomyans for adequate separation of excretory products and respiratory currents.

Sinus and the question of torsion. One of the most evident and commonly discussed trends in gastropod evolution documents the post-torsional modifications of the mantle cavity for efficient manipulation of respiratory currents and elimination of excretory products. In the Bellerophontacea and Pleurotomariacea, fouling of the inhalant currents was presumably circumvented by the development of an anterior emargination

of the mantle into a sinus or slit, permitting separation of the anus from the immediate region of the head. Presence of a sinus or slit has therefore been interpreted as a primary indication of torsion in fossil archeogastropods.

Prior to the discovery of muscle scars in *Sinuitopsis*, all known cyclomyans were easily distinguished from bellerophonts, for, in addition to symmetrical multiple muscle pairs (considered a pre-torsional character), they lacked a sinus. Quite logically then, they found a taxonomic home within the Class Monoplacophora. The presence of a deep sinus in *Sinuitopsis* emphatically demonstrates the need for reconsideration of the basic anatomical relationships of the Monoplacophora and Gastropoda.

Within the framework of our knowledge of the anatomy of early Monoplacophora and Gastropoda the sinus of *Sinuitopsis* is functionally interpretable as the locus of a recessed anus. We are then immediately tempted to question whether the anus was anterior (post-torsional) or posterior (pre-torsional); i.e. was *Sinuitopsis* a gastropod or a monoplacophoran? If we take the view that *Sinuitopsis* is a bellerophontiform gastropod we can explain the sinus (now anterior) in the conventional manner, a response to the problem of fouling. However, we are then faced with the necessity of explaining the symmetrically placed multiple pairs of muscle scars, a radical departure from the documented bellerophontid muscle arrangement—a single pair of columellar retractors (Knight 1947). All the muscle pairs except perhaps the ventrolateral pair would have to have developed after larval torsion to fulfil some highly specialized function.

On the other hand there exists considerable evidence in support of an untorted anatomical reconstruction of *S. acutilira*. There is a lack of parietal inductural deposits, a feature often (perhaps always) present on bellerophonts and interpreted as an excellent indication of torsion, since they are most logically the result of shell deposition over the posterior portion of the foot. The shell microstructure, although inadequately known, appears to be dominantly prismatic and lamellar, but not crossed lamellar as is the case with known bellerophontid shell structure. Finally, the ridge–furrow complex and especially the muscle scar arrangement are typical of cyclomyans that do not bear a sinus.

Evaluation of the evidence suggests to us a posteriorly situated anal sinus in *S. acutilira*, functionally understandable in terms of the achievement of maximum separation of respiratory currents and excretory products.

TAXONOMIC IMPLICATIONS

The existence of a sinus-bearing monoplacophoran necessitates a reappraisal of the taxobases employed in fossil monoplacophorans and archeogastropods. Evaluation of *S. acutilira* suggests that a sinus (or slit) is not a character developed only in response to torsional problems but may have preceded phylogenetic torsion in those early molluscs. Indeed, if this were the case, the fouling situation concomitant with torsion would not have existed, thus giving the newly torted form a selective advantage.

Sole reliance upon the presence or absence of a sinus for the differentiation of monoplacophorans and archeogastropods is no longer justified. The definition of the superfamily Bellerophontacea should be modified to reduce emphasis on the sinus in favour of secondary parietal deposits and posterior trains, since the latter seem better indices of torsion. Concurrently, of course, the morphological conception of the Class Mono-